

THE IBIS.

SEVENTH SERIES.

No. V. JANUARY 1896.

I.—*Remarks on the Stereornithes, a Group of Extinct Birds from Patagonia.* By CHAS. W. ANDREWS, F.G.S.*

THE discovery of the existence of large flightless birds in South America at the time of the deposition of the lower Tertiary strata in that region is one of the most interesting that have been made in recent years, and the abundance and variety of the remains already brought to light give great promise of future large additions to our knowledge of the group.

In 1887 Señor Florentino Ameghino, to whom we are indebted for many papers on the remarkable fossil mammals of South America, described the anterior portion of the lower jaw of a large animal which he supposed to be an edentate mammal, and to which he gave the not very euphonious name *Phororhacos longissimus*. It is perhaps not too much to say that if no further discoveries had been made no one would have ventured to attribute this fragment to a bird. In 1891, however, the same author, having obtained a considerable number of other bones, announced that they belonged to a gigantic bird; but, owing to the incompleteness of his material, some of the characters given, such as the

* Read in abstract before Sect. D at the Meeting of the British Association at Ipswich, on September 13th, 1895.

presence of teeth and of a helmet-like crest on the skull, were incorrect, as he himself has since stated.

In 1891, also, MM. Moreno and Mercerat published a catalogue of the bird remains in the Museum of La Plata, giving a number of photographic plates, but, unfortunately, no descriptions. In this paper many generic names seem to have been employed on quite insufficient grounds. For the reception of the larger, presumably flightless forms, the authors established a separate order, the "Stereornithes," which, again, they divided into four families, Brontornithidæ, Stercornithidæ, Dryornithidæ, and Darwinornithidæ. Probably, also, some of the genera placed by them under the Accipitres belong to this order. The name "Stereornithes" is now generally adopted, and some authors have included under it the Gastornithidæ.

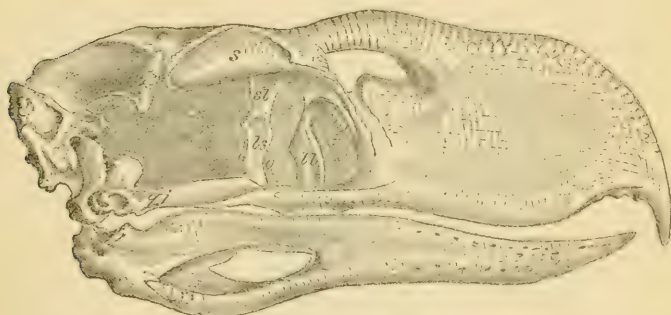
Dr. Gadow considers that the Stercornithes are ancestral forms of the Ratitæ, and further that *Mesembriornis* is the direct forerunner of *Rhea*. Ameghino and Lydekker have also regarded them as Ratites, but the latter, having had an opportunity of examining an incomplete skull, and finding that the quadrate has a double head for articulation with the skull, has changed his opinion and now considers them as modified Carinates. Probably, in the strict sense of the word, many of these birds are "ratite," but the gradual loss of the power of flight and the consequent reduction of the pectoral muscles might lead to the loss of the keel of the sternum in any "carinate" bird.

Up to the present year all these various conjectures as to the nature of these birds were founded on some limb-bones and some very small portions of the skull, but lately Ameghino has published a very valuable paper descriptive of a large series of remains, including the greater part of the skeleton (except, unfortunately, the sternum), of some of these giant birds*. The genus most completely known is *Phororhacos*, and it is to this that the following remarks chiefly refer.

* "Sur les Oiseaux fossiles de Patagonie." Bol. Inst. Geogr. Argent. xv., cahiers 11 et 12. Buenos Ayres, 1895.

The skull of *Phororhacos* (figs. 1, 2) is of the most extraordinary appearance and size, that of the largest species, *Ph. longissimus*, measuring about two feet in length. The cranial portion is much depressed, while the rostral region is much compressed from side to side, somewhat as in the Puffin. The beak is hooked, like that of a raptorial bird, and its margin at the commencement of the decurved portion bears two or three serrations. The orbit is said to be completely continuous with the antorbital fossa. The mastoid processes are very prominent, giving the hinder portion of the skull somewhat the appearance of that of

Fig. 1.



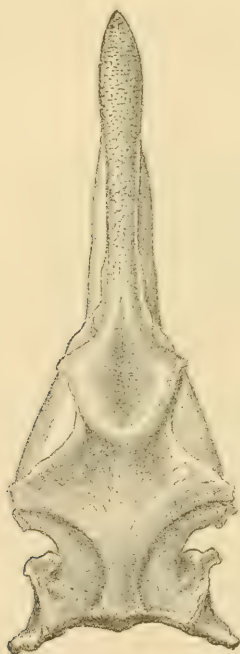
Skull of *Phororhacos inflatus*. $\frac{1}{4}$ nat. size.
(From Ameghino.)

Phalacrocorax, although in most other respects it is quite dissimilar. The temporal fossæ are very large, and are separated one from another only by a short interval. The quadrate is very large, and articulates with the skull by a double head. The mandible is extremely massive; its angle is truncated, as in the Storks, Accipitres, and many other birds. The anterior extremity is upturned: in this respect the mandibles of *Psophia* and *Mycteria* have been compared with the fossil, but in the former only the lower margin curves slightly upward at the extremity, and in the latter, as in the Avocet, although the mandible turns upward it is accompanied by the upper beak, which does not curve down over its extremity. The only living bird which I have been

able to find that resembles *Phororhacos* in this point is the remarkable Stork, *Balaniceps rex*, in which also the beak is extraordinarily large.

It is unfortunate that the ventral surface of the skull is unknown, so that further material must be awaited before the important characters of that region are available for comparison with other forms.

Fig. 2.



Skull of *Phororhacos inflatus* from above. $\frac{1}{4}$ nat. size.
(From Ameghino.)

When it is remembered that the systematic position of many recent birds, the anatomy of which is well known, is the subject of great diversity of opinion, it can hardly be supposed that it will be possible to attain any certainty as to the affinities of these extinct forms, of which even the skeleton is incompletely known. Nevertheless a comparison

with other birds, recent and fossil, may give valuable indications of the probable direction in which the nearest relatives of the extinct species should be sought; but all conclusions derived from such comparisons must necessarily be regarded as only provisional, and subject to revision on the discovery of more perfect specimens.

Comparison of the skull of *Phororhacos* with as much as is known of that of *Gastornis* does not seem to reveal sufficient resemblances to justify the inclusion of the latter in the Stereornithes. The more important differences are:—

(1) The presence of teeth in *Gastornis*, the former statement that these exist in *Phororhacos* having been ascertained to be erroneous.

(2) The small size of the temporal fossæ and the sloping occipital surface of *Gastornis*.

(3) The great length of the parietal region in the European bird, giving the skull an aspect totally different from that of *Phororhacos*.

(4) The presence of a pointed angular process in the mandible of *Gastornis*.

Another point which tells against the association of the Gastornithidæ with the Stereornithes is that, although both are said to occur in the Lower Eocene, the associated mammalian fauna renders it almost certain that the so-called Lower Eocene of South America is of a much later date, and is probably synchronous with some part of the Miocene elsewhere. With regard to *Dasornis* all that can be said is that the cranium is much depressed, as in *Phororhacos*, but the specimen upon which the genus was founded is so imperfect that even its avian nature has been called into question.

The skull in the Ratitæ differs from that of *Phororhacos* mainly in the presence of a single head to the quadrate. The beak, also, is much depressed, except in *Casuaris* and *Apteryx*, and the nostrils impervious. The angle of the mandible is truncated, as in the Stereornithes.

The skulls of *Hesperornis* and *Ichthyornis* are sharply separated from that of *Phororhacos* by the possession of

teeth, and are different in many other respects. It may here be remarked that *Hesperornis* cannot be an ancestral form of the Stereornithes, since it is already too specialized (*e. g.* in the extreme reduction of the wings).

In his description of the skull Ameghino lays much stress on the fact that the orbit is not at all separated from the antorbital fossa; but since the lachrymal is commonly very loosely united to the skull, it might easily have been somewhat displaced in the fossil, and it may be suggested that the bone described as the supraorbital may, in fact, be the lachrymal. The descending lamina, marked *sl* in the figure (p. 3), would then correspond to the descending process of the lachrymal, which in most birds forms a more or less complete division between the orbit and antorbital fossa, as in many birds this process unites inferiorly with the jugal. The bone marked *ll*, and regarded as a descending portion of the lachrymal, would then probably be a portion of the ethmoid. In this region of the skull of *Phororhacos* there seems to be a certain resemblance to that of the Seriema (*Cariama*). In this form also the lachrymal sends down a branch, which is connected with the jugal by a small distinct rod-like element, described long ago by Burmeister* and apparently occurring in *Cariama* only. In Ameghino's figure there is some indication that the element marked *ls* may also be distinct; and if it should turn out that this is the case, it would be a point of some interest. In *Cariama* also, in front of this boundary of the orbit and at the bottom of the antorbital fossa, there is another vertical bar of bone, which consists of a portion of the ethmoid and would correspond with that marked *ll* in the figure. In *Psophia* the lachrymal is small and does not extend to the jugal. In both *Psophia* and *Cariama* the angle of the mandible is truncated. In *Cariama* the nostrils are pervious, as they also appear to be in the fossil, although the septum may have been lost. In *Chauna* also the lachrymal is small and does not extend to the jugal, and the mandible has a very large angular process. *Cathartes*, again, differs in many respects, though in the form of the nostrils

* "Beitr. z. Naturgesch. d. Seriema," in Abh. nat. Ges. z. Halle, i. p. 11 (1854).

and the outline of the upper mandible there is some likeness to *Phororhacos*.

The vertebræ have articular faces of the usual avian form. They are penetrated by pneumatic foramina, and the dorsals and some of the cervicals bear median hæmapophyses. The most remarkable point is that some of the dorsals and all the caudals have their centra perforated by a remnant of the notochord. The posterior caudals, which are said to be procœlous, do not unite to form a pygostyle; this character, as in the Ratitæ, is probably "pseudoprimitive." In *Hesperornis* also the posterior caudals do not unite, but in this case their elongated transverse processes convert the tail into a paddle-like organ quite unlike that of *Phororhacos*.



Pelvis of *Phororhacos inflatus*. $\frac{1}{6}$ nat. size.
(From Ameghino.)

The pelvis of *Phororhacos* (figs. 3, 3 a) is remarkably long and narrow, and at first sight has some resemblance to those of *Hesperornis* and *Colymbus*, but on comparison is found to differ in nearly every point. For example, in neither of these birds do the pre-acetabular portions of the ilia unite in a crest above the neural spines. In *Hesperornis* the

ischium does not unite posteriorly with the ilium nor the pubis with the ischium. In *Phororhacos* the pubis is very small, and indeed, except for the short distance during which it forms the inferior boundary of the passage for the *obturator internus* muscle, it fuses with the lower border of the ischium, beyond which it does not seem to have extended, although the posterior prolongations may have been broken away. The compressed form of the pelvis and the elongation of the post-acetabular portions of the ilium are notable. Prof. Milne-Edwards has remarked that the larger the pre-acetabular ilium the better a bird is adapted for walking, while the post-acetabular portion increases in length in proportion as the bird is better adapted for swimming. This, no doubt, is generally true, and is well illustrated in *Hesperornis* and *Podicipes*, in the former of which the post-acetabular ilium is about three times the length of the pre-acetabular portion, and in the latter about twice as long. In *Phororhacos* the proportions are nearly as in *Podicipes*, but, considering its long powerful legs and digits provided with hooked claws, it is difficult to imagine that it was a good swimmer. The pelvis of *Cariama*, though shorter and broader in the post-acetabular region, is nevertheless somewhat similar to that of *Phororhacos*, and this likeness is more striking when the pelvis is viewed from the side. The relation of the ischium to the ilium is exactly similar, and the pubis, which is extremely slender, is closely applied to the ventral border of the ilium, with which, however, it is not co-ossified in the specimen examined. The posterior extremities of the pubes extend beyond the ischia and are expanded: in the fossil these may easily have been lost. The pelvis of *Psophia* is not so similar, and those of the Tinamou and of *Cathartes* are still more unlike.

The femur is long, straight, and comparatively slender. The head rises above the slightly developed trochanter; in this respect the bone is similar to that of *Gastornis* (although in that bird the trochanter is much larger) and *Phalacrocorax*. In *Grus*, *Cariama*, *Psophia*, and *Aptornis* the trochanter is largely developed and rises above the head. In

Chauna and *Cathartes* the neck is exceedingly short and stout, and the distal extremity slightly expanded. In all the Ratitæ this bone is considerably stouter in proportion to its length and differs in other respects.

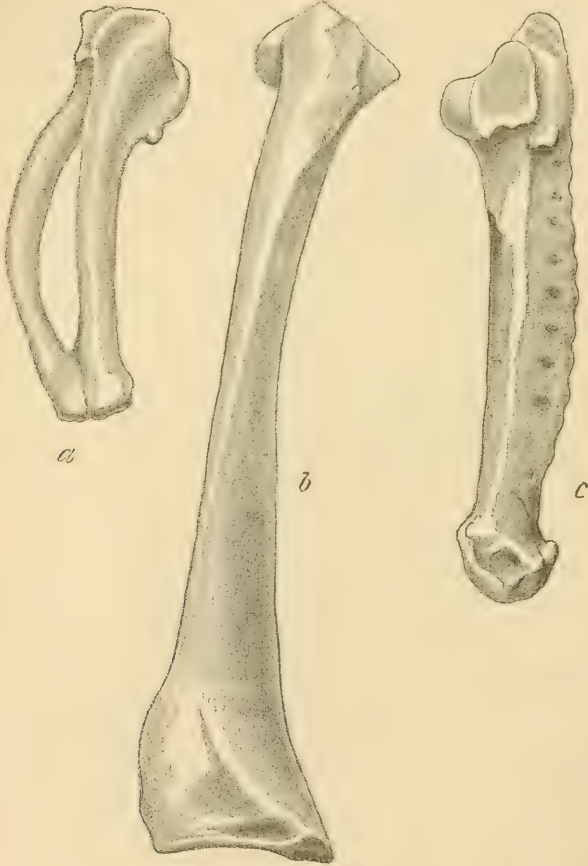
The tibio-tarsus of *Phororhacos* is about twice as long as the femur, and is straight and slender. The distal condyles are subequal and the intercondylar groove is shallow. The bridge over the groove for the extensor tendons lies towards the inner border of the bone and is somewhat oblique. In *Cariama* the tibio-tarsus is more slender and is more than twice the length of the femur. The extensor bridge is somewhat less oblique, and the intercondylar groove is shallower than in the fossil. The crest for the attachment of the fibula (not shown at all in the figure of the fossil) is prominent. The tibia is considerably different at its lower end from that of *Gastornis*, in which the bridge is median, the groove deep, and the lower end as a whole somewhat inflected, closely resembling that of an Anserine bird. In all the Ratitæ the intercondylar groove is shallow, and except in the Dinornithidæ the extensor bridge is wanting. In some of the smaller members of the latter genus the resemblance to the fossil is considerable.

The metatarsus and, indeed, the tibia also of *Phororhacos* have already been compared with the corresponding bones in the Ratites and in some of the Carinates by Dr. Gadow. Here it will be sufficient to mention that in the structure of the hypotarsus and in the arrangement of the distal trochleæ it agrees in some respects with *Cariama*. In this bird, however, the bone as a whole is more slender than in *Phororhacos*. The latter, in the whole structure of the limb, differs widely from *Hesperornis* and *Colymbus*, to which the form of the pelvis might lead one to expect some similarity. From *Cathartes* and the Tinamou there are also great differences. The digits of *Phororhacos* are provided with powerful hooked claws unlike those found in any of the Ratitæ.

The coracoid (fig. 4, *b*, p. 10) is remarkably long and slender. In general form it resembles that of some Gallinaceous birds; in any case it is quite unlike that of any of the Ratitæ, in

which this bone is usually broad and flat, and possessed of a more or less well-developed precoracoid process (except in *Apteryx*, in which it is rudimentary). This great difference

Fig. 4.



Phororhacos inflatus. $\frac{3}{4}$ nat. size.
 a. metacarpus; b. coracoid; c. ulna.
 (From Ameghino.)

in the form of the coracoids constitutes, in my opinion, one of the greatest difficulties in the way of supposing that the Ratitæ are descended from these extinct forms. The Ratite

shoulder-girdle seems more primitive, and it is difficult to suppose that its condition is secondary and due to retrogression, or, in other words, that it is "pseudoprimitive." In most of the Gruiformes the coracoid is short and stout, but in *Cariama* the bone is comparatively slender and the hyosternal process reduced.

The humerus in *Phororhacos* is much reduced, and is short and stout. The upper end is not figured, but the lower is remarkable for the obliquity of the distal border, the inner margin being prolonged into a pointed process which extends below the articular surfaces. The distal extremity is somewhat similar to that of the humerus of *Aptornis*, which also is oblique, but without the acute internal angle. The continuity of the articular surfaces is probably merely the result of reduction; the same condition is well shown in the humerus of *Casuarinus*.

The ulna (fig. 4, c) is short, stout, and compressed. The tubercles marking the points of insertion of the secondaries are strongly developed: these do not occur in the Ratitæ. There is a well-developed olecranon process.

The metacarpal (fig. 4, a) is of the usual avian form, but as in some Ratites the distal ends of metacarpals 2 and 3 are not so firmly fused as in most Carinatae.

The wings of *Phororhacos*, though so much reduced that the power of flight was almost certainly wanting, were nevertheless powerful organs with apparently well-developed remiges. Most likely they were employed as aids in running or possibly in swimming, though the latter seems unlikely.

Señor Ameghino unfortunately does not state upon what evidence the various bones are referred to *Phororhacos*, but, assuming that they are correctly determined*, the comparison given above shows that there is not much reason for supposing that any close relationship exists between *Phororhacos* and the Gastornithidæ, and the difference of the age of the deposits in which they respectively occur renders such relationship the more improbable.

* I have lately been informed that the bones described under the name *Phororhacos inflatus* nearly all belonged to a single individual.

The Ratitæ are in many respects more primitive, and not improbably were already sharply separated from the Carinatae when the Stereornithes arose.

The absence of specimens of the Stereornithes from European museums is much to be regretted, since without actual examination of the bones it is rash to express any definite opinion as to the affinities of the group. Nevertheless, in the meantime it may be suggested that some at least of the Stereornithes may form a specialized offshoot of the stock which gave rise to the Neotropical Gruiformes: possibly some affinities to the Ralliformes may also be found.

Besides *Phororhacos*, Ameghino describes several other genera, including *Brontornis*, *Pelecyornis*, *Liornis*, and *Callornis*, but, in the absence of sufficient material, much less completely. Most likely the number of genera will have to be increased by the retention of some of those founded by Moreno and Mercerat, which have been placed by Ameghino among the synonyms of *Phororhacos*—e. g., *Dryornis*, of which the humerus, as figured, is totally unlike that of *Phororhacos*. Certain of these genera differ so widely one from another that their reference to distinct families seems quite justifiable. Indeed, the Stereornithes seem to be a heterogeneous group of birds in all of which the wings were reduced and the bulk increased through the operation of some peculiar local conditions; for instance, the land which they inhabited may have been an island on which no large carnivorous animals occurred. A similar example is offered by New Zealand, where the Dinornithidæ, *Apteryx*, *Aptornis*, and *Cnemionis* (all flightless birds of large size, belonging to several distinct orders) were formerly found. Indeed, there seems no reason why at any time, from the late Secondary period onward, and in any region, similar groups of flightless birds might not have arisen under favourable circumstances. The Gastornithidæ may be another instance of such. In most cases such specialized races die out without leaving any descendants when the peculiar conditions to which they have become adapted pass away; but the modern Ratitæ may be survivors of one or several ancient groups of such flightless birds.